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On the transpiration of Fouquieria splendens*

WILLIAM AUSTIN CANNON

The present paper is an account of one of several studies which were carried on in 1904 by the polymeter method upon plants in place. It will not be necessary to give here a description of the method, since this will soon be done elsewhere,† but a certain peculiarity attending its use may be briefly referred to. By the new hygrometric method it is possible to study the transpiration of a plant in the field not only once, but many times, without injury to it. The fact that repeated observations of transpiration can be made rendered it possible to learn not only the daily but the seasonal rate as well. Thus a transpiration history, not indeed without many gaps, has been traced. The experiments were begun in February and were continued from time to time until after the rains of summer were over.

In addition to the transpiration observations, and in connection with them, certain environmental factors were observed and measured and a comparison was made between them and the rate of transpiration. This part of the work was from necessity secondary, but despite this enough was done to establish certain important facts and to indicate lines of study which may be profitably followed in the future.

The difficulty in tracing the influence of external conditions on the rate lies, among other things, in the changeableness of these

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* Papers from the Desert Botanical Laboratory of the Carnegie Institution, No. 10.

† Cannon, W. A. A new method of measuring the transpiration of plants in place. Annals of Botany, *ined.*

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factors from day to day. For outdoor work, therefore, where the conditions cannot be controlled beyond a certain limit, it is a great advantage when the climatic factors vary in a uniform manner, or when certain conditions are so pronounced that their influence is unmistakable. The year 1904 was an especially fortunate one for field work because, as will be shown below, uniform variations in the temperature of the air, in humidity and in other climatic features were maintained for days together, and the uniformity of the environmental factors made the outdoor work similar in this regard to that done in the laboratory where the conditions of experiments are to a degree under control.

Apparently the main cause of the uniformity of the climate in 1904 was the small rainfall of the year. At the same time the most disturbing feature of the uniformity was the sudden and infrequent rains. Since the rain is an all-important factor in the biology of desert plants, it consequently happens that the history of their transpiration reflects most clearly the influence of rain and of drought, so that the relation of transpiration to these features constitutes the key-note of the studies. For this reason it is best before presenting an account of the experiments to give an outline record of the climate for the year, in which emphasis is placed on the humidity of the air and on the rainfall.

CLIMATE FOR 1904

The normal rainfall at Tucson, the average for 15 years, is 11.74 inches.* In 1904 the total precipitation was 7.79,† or about 75 per cent. normal.

The distribution of the rains throughout the year, both the usual distribution and that for 1904, is shown in FIGURE 1. It will be observed from the figure that the winter rains of the year were very light, but the summer rains, particularly those of August, were slightly greater than usual. This distribution operated therefore to intensify the dryness of that portion of the year when the plants are naturally least active, and at the same time to bring about unusually favorable vegetative conditions at the season of the greatest activity, that is, in summer.

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* Coville, F. V., & MacDougal, D. T. Desert Botanical Laboratory of the Carnegie Institution, 26. 1903.

† From data provided by the University of Arizona.

The significance of the small rainfall of the year is a factor which must be taken into account, and, although it seems difficult to express this concretely, it may be better appreciated if we consider the relation of the precipitation of the year to the possible total evaporation. The normal annual evaporation at Tucson is estimated to be 90 inches.* The ratio between the normal annual rainfall and the evaporation is therefore 1 : 7.7. If we suppose for the moment that the decrease in 1904 of approximately 25 per cent. in the precipitation was accompanied by a proportional increase in the evaporation for the year, the ratio would be greatly altered. An increase of 25 per cent. in the total evaporation would make 112.5 inches ; and the ratio between precipitation and evaporation becomes 1 : 12.7.

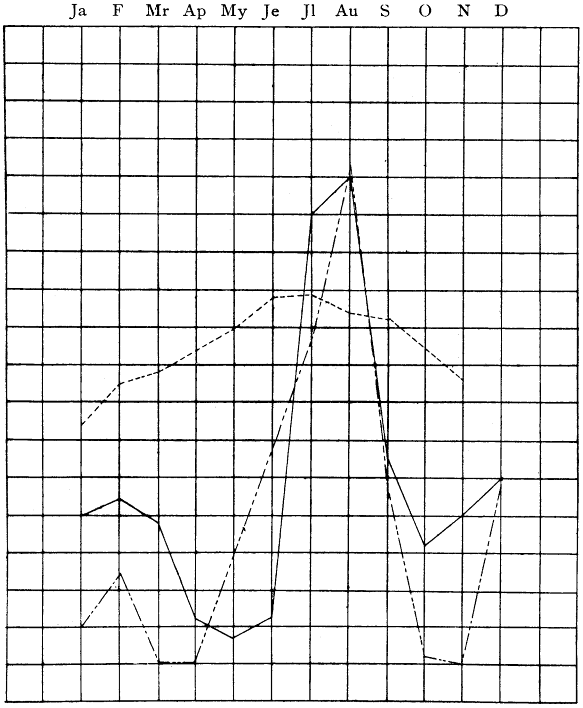

FIGURE I. The rainfall and the mean maximum temperature at Tucson. The normal rainfall is represented by a solid line ; the rainfall in 1904 by a broken one (- - — - -) ; 5 mm. = one-half inch precipitation. The mean maximum temperature for the year is given by the second broken line (- - - - -) ; 5 mm. = 10 degrees Fahrenheit.

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* Coville & MacDougal, *l. c.* 27.

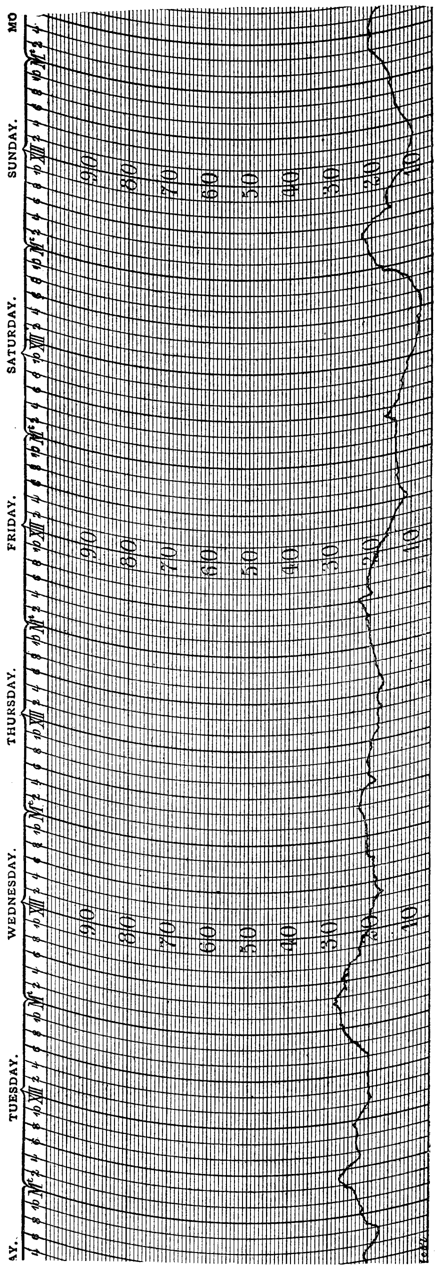

FIGURE 2. Hygrographic record for the week ending July 4.

Whether the amount of evaporation for 1904 and the relation of that amount to the rainfall of the year as given are exact expressions of the true ratio and of the actual amount does not matter for the present — the striking fact, which is inadequately shown by the illustration, is that a really small decrease in the annual rainfall may be a most important fact in the nicely balanced life relations of desert plants.

A climatic condition, the relative humidity, which is closely associated with the rainfall and thus with the rate of transpiration, may be passed over in few words. As the seasonal rainfall was less than usual, so also the average relative humidity was probably correspondingly lower. What the departure from the normal may have been, however, I have no observations at hand to show. Certain it is that the humidity at times was very low, as for instance during the entire week ending July 4 it did not even at night-time exceed 28 per cent. In the daytime it was always low (FIGURE 2).

A certain peculiarity of the changes in the relative humidity, which may have to be taken into account when the biological significance of the absorption of water by the aerial parts is considered, may be pointed out. I refer to the fall of the humidity which ordinarily occurs soon after a storm has passed. This is illustrated in FIGURE 3. On Wednesday night, Thursday and Thursday night a small rainfall (.04 in.) occurred. During the rain the humidity was rather high even in the laboratory where the hygrograph was placed, but within twelve hours after it ceased the humidity was nearly as low again as previous to the storm.

The humidity remains high, however, for several days following a long storm, and since the most rain ordinarily falls in summer this peculiarity cannot fail to be of great importance to the desert plants.

As regards the temperature it will not be necessary for the present purpose to go into this phase of the climate of the year more than to mention certain striking characteristics.

The annual as well as the daily range was relatively large. During the driest portion of the summer, in June, the maximum for the year, 107° F., was recorded. The temperatures were somewhat lower after the rains of summer had come. (See FIGURE 1, which shows the mean maximum temperature for 1904.) In the colder part of the year, December to March, the thermometer reached the freezing point or below each month, and in January a temperature of 15° F., which was the minimum for the year, was reported. The range of temperature for the year was therefore 92° F.

Fifty degrees Fahrenheit was the greatest daily range. This was recorded in April in the midst of a rainless period. In August, on the other hand, during the summer rains, a daily range of but 31° F. was noted — this was the least of the year.

FOUQUIERIA SPLENDENS

Fouquieria splendens, "ocotillo" of the native Mexicans, is one of the most striking desert shrubs. It is well adapted, not only in the mature condition but as a seedling as well, to endure

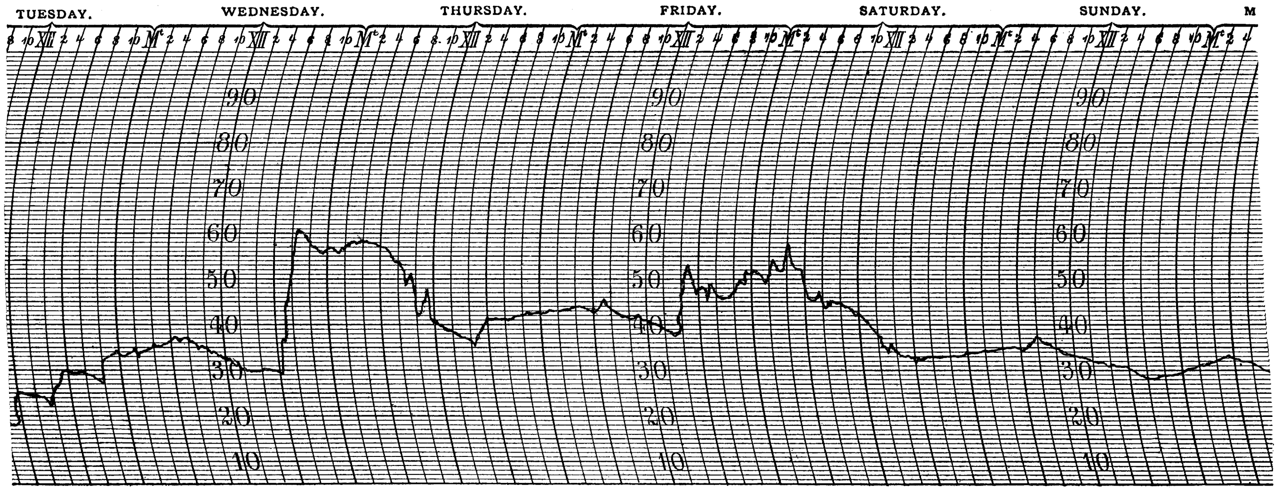

FIGURE 3. Hygrographic record for the week ending June 20 The figure shows a characteristic rise in humidity during a sudden storm and a characteristic fall after the storm has passed. In this instance the rain (.04 in.) occurred on Wednesday, at night, and on Thursday.

droughts apparently the most extreme, and it flourishes in habitats which are so dry as to be unfit for many desert plants.

A characteristic specimen of ocotillo is composed of a number (a dozen or more) of fairly straight branches, for the most part simple, which arise from the short main stem near the ground (FIGURE 4). The branches are from 2 to 5 meters in length, and bear spines which are regularly placed and which are morphologically midribs of the primary leaves.

During the dry seasons the branches are naked, but in the rainy ones they are well covered with rosettes of small leaves which are borne in the axils of the spines. The variation in the foliage is not a seasonal phenomenon but is directly associated with the distribution of the rainfall. Although seemingly lifeless during the droughts the plant is not dormant, since beneath its gray exterior there is chlorophyl-bearing tissue which enables the photosynthetic processes to go on, even if in a feeble manner, and consequently some transpiration may always be detected. When the rains return new leaves are formed with a promptness that is

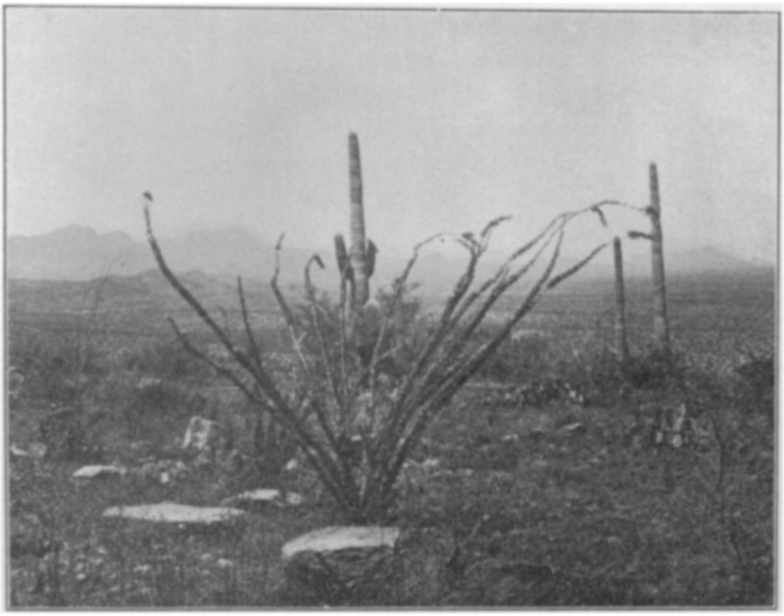

FIGURE 4. *Fouquieria splendens* in leaf.

surprising, and this phase of the plant's history constitutes one of the most admirable of adaptations to desert conditions.

RECORD OF EXPERIMENTS

All of the experiments on *Fouquieria* which are reported in this paper, but which constitute a part only of those performed, were conducted with the polymeter method of determining transpiration already mentioned,* and all were conducted upon plants or branches in place. It will only be necessary for the sake of clearness to point out the significance of the figures under the heading "Amount in milligrams." In each instance the first number refers to the amount of moisture present in the bell-glass, which encloses the plant, at the beginning of the experiment; the second number is the amount of moisture in the bell-glass at the end of the experiment. The difference between the two numbers constitutes of course the amount transpired in the time expressed in the first column.

TRANSPIRATION OF FOUQUIERIA No. I. EXPERIMENTS 1–6

Fouquieria No. I is growing about 150 meters south of the laboratory building. It has half a dozen branches and is about one-half a meter high. The first three experiments were performed when the plant was leafless, because of the severe drought; leaves were present in the other experiments.

Experiment No. 1, February 12: Transpiration of leafless stems

The following data were derived from this experiment:

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
10:30	23.5	78° F.	65
12:30	27	81	68.5

Experiment No. 2, February 15: The same

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
11:40	28.5	77° F.	63.7
1:40	31	79	73.7

The rate of transpiration in Experiment No. 1 is 1.85 milligrams per hour; that in the succeeding experiment is 5 milligrams per hour.

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* Cannon, *l. c.*

A slight rain, not enough to induce the formation of leaves, was recorded previous to the 12th. From subsequent experiments on the influence of the rains on transpiration it was observed that the rate may be increased without a change in the extent of the transpiring surface, and it is possible that the small but positive change in the rate which was recorded in Experiment No. 2 is directly traceable to the earlier rain.

In the experiments on the naked stems of *Fouquieria* it was suspected that the hygrometric method did not reveal the true condition of affairs inasmuch as it did not show how much of the moisture which had been evolved from the plant was subsequently absorbed by the dry branches. The affinity of air-dry stems of *Fouquieria* for atmospheric moisture had been demonstrated in the laboratory in the following manner: Leafless branches were removed from the plant, the cut end was coated with vaseline and the branch was placed in a beaker containing about two centimeters of water. The water very promptly ascended for several centimeters the surface layers of the branch, which also increased considerably in weight. The same behavior of leafless stems was also observed outdoors. In every instance the portion of the stem which had the affinity for water was the *younger* portion. Later the outer cortical part of the branches is infiltrated with a waxy substance which is impervious to water. To learn whether air-dry stems would absorb water-vapor also the succeeding experiment was devised.

Experiment No. 3, February 16: Absorption of hygroscopic moisture

The apparatus was set up in the same manner as if to determine the transpiration but with the addition of an arrangement by which air charged heavily with vapor was made to pass into the bell-glass. As soon as the humidity of the air of the bell was increased sufficiently, the openings into it were tightly closed and the reading of the polymeter was taken. The following is a brief of the experiment.

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
10:25	65	83° F.	176
11:15	53.5	88	168.7

In 50 minutes the stems absorbed 7.3 milligrams of moisture.

Although this experiment and others not reported indicate that under certain conditions leafless branches of *Fouquieria* can and in fact do absorb appreciable amounts of water and of water-vapor, they do not show that the water or the vapor is of physiological significance. Whether such is true I have not been able to demonstrate; since all the evidence thus far accumulated is negative.

Experiments 4–6: Effect of rains

The immediate effect of rains upon the rate of transpiration was repeatedly observed. When they resulted in an actual increase in the water-supply of the plant, the rate became greater, and later, as the available water-supply was decreased, the rate of transpiration became smaller. This was shown by the experiments on February 24 and March 4, 10, and 17, when leaves were developing, when they were mature, and when they may be termed senile. The rates for these experiments were respectively 47.5, 120, 24.4, and 13.7 milligrams per hour.

The intimate connection of the rate with the rains is also shown, and more strikingly, in the experiments which were performed soon after the rains of May. Between the experiments which were carried on during the latter part of March and those of May the plant was defoliated on account of the continuation of the drought. The rains of May were distributed as follows: May 10, .47 in.; May 11, .75 in. (the latter fell between 1:40 and 2:15 P.M.); May 12, .02 in. and May 16, .06 in. As a result of this sudden and considerable rainfall the mountain upon which the Desert Botanical Laboratory is situated, which had been very dry all winter, was thoroughly wet, and the mesa between it and the Santa Cruz River was covered with water. This rain had a very marked effect upon all vegetation. Trees and shrubs which had been without leaves all winter put out leaves promptly, the cacti which had become badly shriveled from loss of water directly became plump, but perhaps the most noticeable response was given by the fouquierias. Up to the time of this storm *Fouquieria* No. I and other ocotillos were leafless. On Friday, May 13, 48 hours after the heaviest fall of rain, *Fouquieria* No. I was rapidly coming into leaf, and by the afternoon of the following day these were of nearly mature size. The three succeeding experiments were performed Friday, Saturday and Monday — May 13, 14, and 16 — and they illustrate how promptly the plant availed itself of the more favorable water-supply.

Experiment No. 4, May 13

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
2:55	33.5	93°F.	122.5
3:05	49	93	180

The rate is 345 milligrams per hour.

Experiment No. 5, May 14

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
9:48	30	91°F.	103.7
9:56	66.5	94	231.2

The rate is 956.2 milligrams per hour.

Experiment No. 6, May 16

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
9:15	25	92°F.	88.7
9:20	66.5	93	245

The rate is 1875.6 milligrams per hour.

Summary of experiments on Fouquieria No. 1

			Transpiration in milligrams per hour.
February	12	(without leaves)	1.8
"	15	"	5
"	24	(in leaf)	47.5
March	4	"	120
"	10	"	24.4
"	17	"	13.7
May	13	"	345
"	14	"	956.2
"	16	"	1875.6

TRANSPIRATION OF FOUQUIERIA NO. II. EXPERIMENTS 7–9

Fouquieria No. II, which is growing nearly north of the laboratory and a little lower on the mountain, is about the size of *Fouquieria* No. I. The character of the plant and the general nature of the habitat are indicated by FIGURES 5 and 6, and do not require further comment.

Experiment No. 7, March 22: Effects of irrigation

At this time the leaves of *Fouquieria* No. II, as of others on the mountain (see Effect of rains, page 406), had been nearly all discarded and most of those which remained were yellowish or partly withered and plainly indicated the harmful effects of the prolonged drought. The rate of transpiration was also very small, as the data of an experiment taken in the midst of the dry time shows.

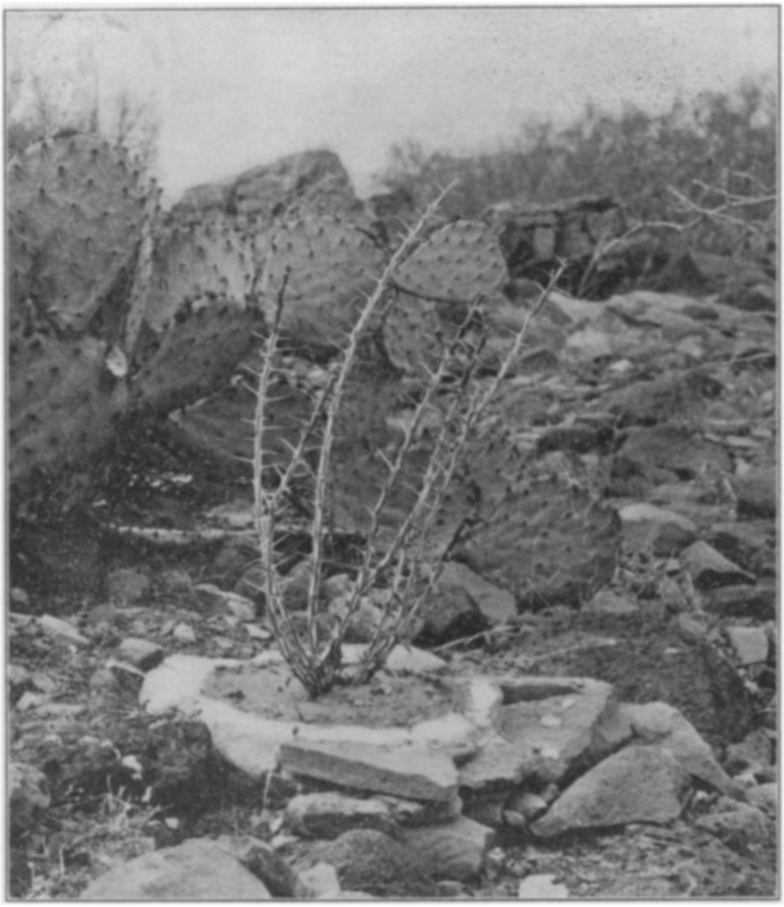

FIGURE 5. *Fouquieria* No. II, March 26.

The following data were derived from an experiment which was conducted before water was given the plant.

Time.	Per cent of saturation.	Temperature.	Amount in milligrams.
1:30	55	80° F.	208.7
2:30	68	79	323.7

The rate of transpiration is .22 milligrams per minute for 100 sq. cm. of leaf surface, or 115 milligrams per hour for the entire plant.

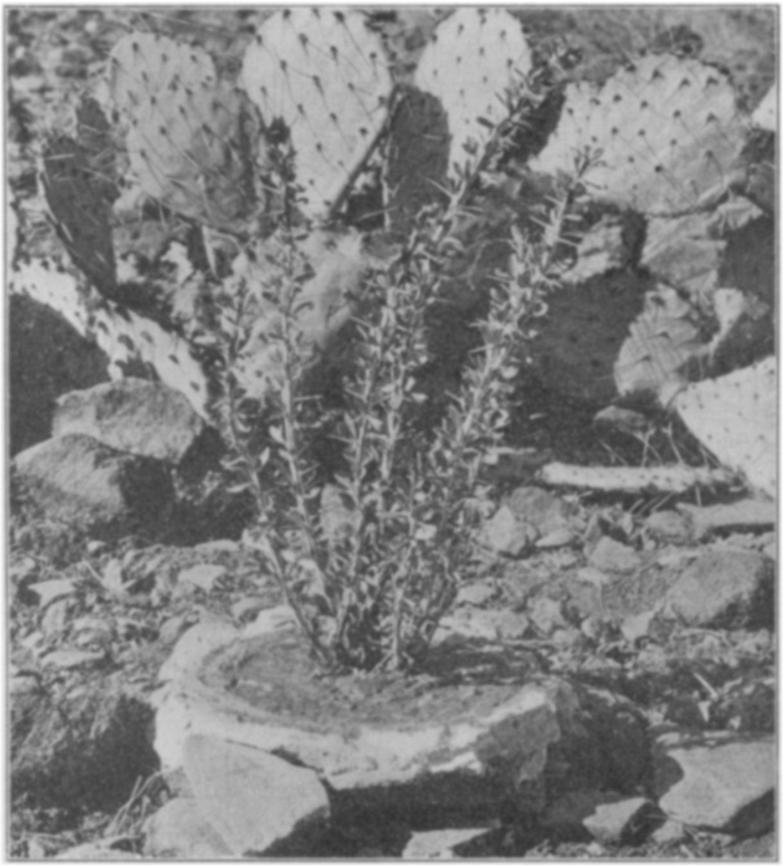

FIGURE 6. *Fouquieria* No. II., April 8. This plant was without leaves, March 26 (*Figure 5*); it was given water March 26 and March 28 and was in leaf April 4.

Experiment No. 8, April 5: The same

To watch the reaction of the plant to an increase in the water-supply, at a time when it was suffering from an insufficient supply,

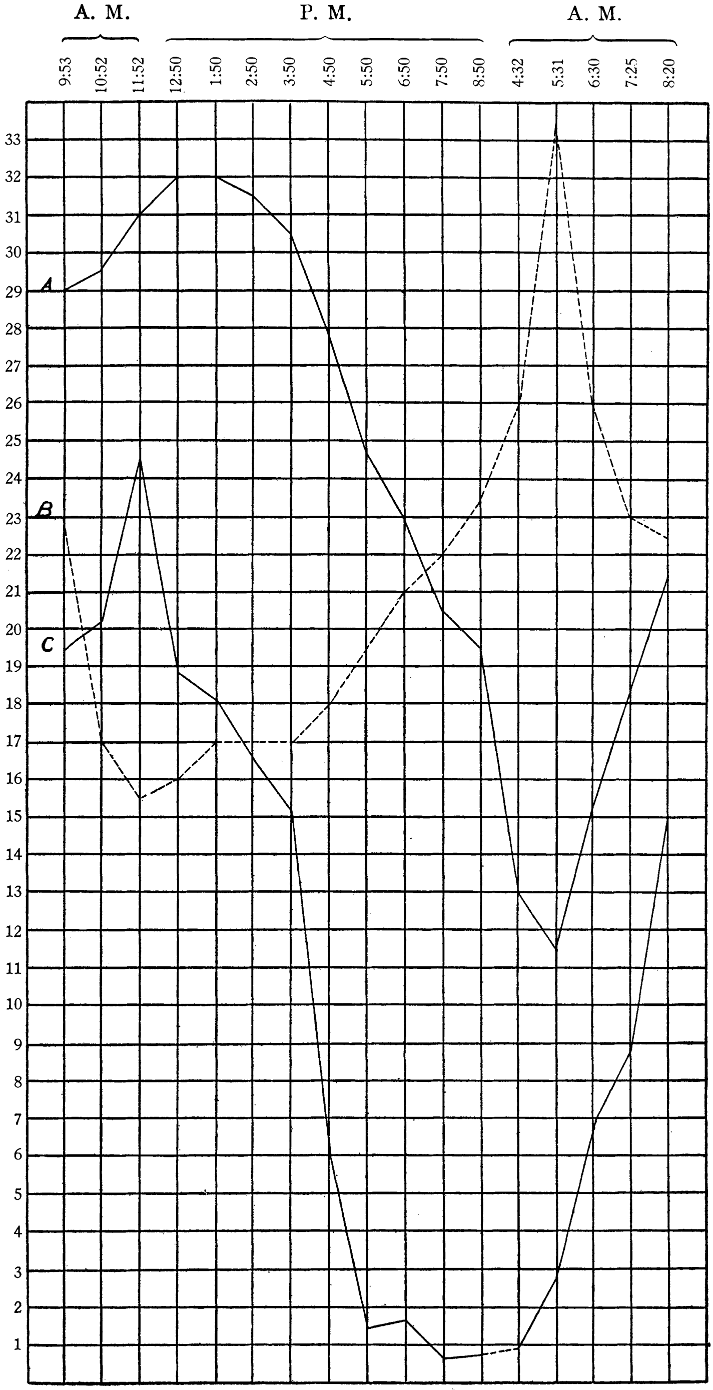

FIGURE 7. Daily periodicity in *Fouquieria*. *A* = temperature of air in degrees Centigrade. *B* = relative humidity, taken before each experiment. *C* = transpiration calculated to hourly periods, each space representing 100 milligrams. The time of each reading is given.

on March 26 and 28 about 20 gallons were put slowly on the ground at its base. As a result leaves were put out very promptly and the total transpiration was increased many fold.

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
10:03	28	26° C.	133.7
10:13	72	27	382.5

The rate of transpiration is 1492.8 milligrams per hour for the entire plant.

The history of the leaf-covering of *Fouquieria* No. II from February to August is of interest. The plant was seen to be in leaf the latter part of February, but as a result of the long drought in March the leaves fell away, so that the foliage which the plant formed the first part of April after it had been irrigated (Experiment No. 8) was the second leaf-covering of the year. April was a dry month and the plant was again defoliated. The drought was broken by a rain about the middle of May and *Fouquieria* No. II came into leaf for the third time. With the advent of dry and hot weather in June the leaves fell away again. On June 29 three gallons of water were poured slowly on the ground at the base of the plant. Leaf-buds were observed July 1, and at 2 P. M. on the succeeding day they were 1 cm. long. On the fifth the leaves were of mature size. (Compare FIGURE 6.) The leaves which were formed at this time, during an extremely dry season (FIGURE 2), soon withered and the plant was defoliated the fourth time. It is of interest to note that with the coming of the summer rains still another leaf-covering appeared on the plant, and therefore, it happened that *Fouquieria* No. II came into leaf five separate times between February and August, and that the exciting cause in each instance was an increase in the available water-supply.

Experiment No. 9, April 6 and 7: Daily periodicity

On the morning of April 6, at 9:53, the rate of transpiration of *Fouquieria* No. II was taken and it was observed at hourly intervals throughout the day until 8:52 P. M. The experiment was continued the following morning at 4:32 and readings were made every hour until 8:20 A. M. The record of transpiration was complete for the daytime and for a portion of the night. A summary of the experiment is presented in FIGURE 7.

It will be noticed that the curve of transpiration reaches its highest point about noon and that in a general way it is similar to the curve expressing the temperature and that it opposes that representing the relative humidity. However, it neither closely follows the one nor flatly opposes the other. The maximum transpiration precedes the highest temperature of the day and a marked decline in the rate of transpiration takes place while the high temperature is maintained. The opposition of the curves representing the relative humidity and the transpiration is more consistent, but even in this case the afternoon decrease in the rate is more rapid than the rise in the relative humidity. It would be of much interest to compare the periodicity with the daily variation of other factors, as the temperature of the ground, and particularly the daily variation of the light, but unfortunately no data were available at the time to make this possible.

EXPERIMENT NO. 10, AUGUST 26: MAXIMUM RATE

As graphically shown in FIGURE 1, the heaviest rain of the year occurred in midsummer at a time when the temperature also was high. Although the rains did not extend over a period exceeding six weeks, the face of the desert was wholly changed because of them. Annuals in great variety and in large numbers appeared on previously barren stretches, and shrubs and trees which were apparently dormant during the droughts became covered with an abundance of large leaves. Thus the summer vegetation which appeared in consequence of the rains was tropical in its luxuriance. It was with much interest, therefore, that I observed the transpiration of plants at this period.

The following data were obtained about the close of the rainy period from the study of a branch in place:

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
1:10 P. M.	33	98° F.	263.7
1:24	58.5	103	540

The rate of transpiration is 8.25 milligrams per minute for 100 sq. cm. of leaf surface. This is the highest rate observed for *Fouquieria* at any time during the year.

SUMMARY AND CONCLUSIONS

The leading points in this paper together with the conclusions may be briefly stated as follows:

1. The noteworthy feature of the climate of 1904 was the small precipitation, which was 75 per cent. normal. The rainfall was so distributed that little of it occurred in winter, spring or early summer, most of it coming in midsummer. Thus during most of the year the conditions of plant life were very severe; but in August especially they were favorable to plant growth.

2. The customary fleeting vegetation of late winter and of spring, composed mainly of annuals, did not appear, and the larger and long-lived forms either did not put on leaves at the time at all, or if they did so they were dropped when droughts returned. In summer, however, all vegetation was very luxuriant.

3. Although without leaves during periods of drouth *Fouquieria* nevertheless maintains at such times a feeble rate of transpiration.

4. Air-dry stems of *Fouquieria* in place can absorb hygroscopic moisture in appreciable amounts.

5. The rate of transpiration of *Fouquieria*, and of other shrubs, varied directly with the water-supply. The rate increased as an immediate effect of the rains and it decreased as the time past the rains became greater. Accompanying the increase in rate there was always an increase in the transpiring surface (although the rate may increase without the latter), but a decrease in the rate occurred without an immediate and corresponding decrease in the transpiring surface, although in the end this always became less.

6. The least rate of transpiration, when leaves were present, was observed during the dry and cool period the latter part of March. At this time a rate of .22 milligram per minute for 100 sq. cm. of leaf surface was recorded. The highest rate was observed August 26, near the close of the summer rains when the temperature was high. The August rate for the same time and area as in March was 8.25 milligrams.

7. A very striking adaptation to desert conditions is to be found in the promptness with which *Fouquieria* forms leaves when the water-supply of the plant is increased by the rains. As an example of this the following instances may be presented: For several weeks previous to the 11th of May one of the plants

studied had no leaves. Within 48 hours after the rain of May 11 it was well covered with them. On June 29, in the midst of a very dry period, three gallons of water were given to one specimen of *Fouquieria* and leaf-buds were observed on July 1, which by 2 P. M. on the succeeding day were 1 cm. long. On the fifth they were of mature size.

Fouquieria No. II formed five distinct leaf-coverings between February and August. The exciting cause in each instance was an increase in the water-supply. Very soon after the rains were over the leaves were dropped and excessive and destructive transpiration was thus avoided.

8. The daily periodicity of *Fouquieria* was observed in April. The rate varied in a manner corresponding to variations of the temperature, but not quite the same, and it inversely followed very closely the variation of the relative humidity.

DESERT BOTANICAL LABORATORY,
TUCSON, ARIZONA.